head (Grh) late in embryogenesis. Neuroblasts continue to express Grh throughout larval stages of development. Type I neuroblasts lacking Grh undergo premature terminal division, whereas type II neuroblasts lacking Grh do not undergo apoptosis but continue to proliferate. It seems that, rather than affecting the proliferative machinery directly, Grh ensures that neuroblasts undergo their correct lineage-specific temporal program. Therefore, both early and late temporal inputs are required to ensure timely exit from the cell cycle. An embryonic pulse of Cas expression is needed to activate Grh, whereas subsequent expression of Svp, and down-regulation of Cas in larvae are needed to end proliferation at the correct time. Interestingly, disrupting Grh expression in larval neuroblasts has no effect on the switch from Chinmo$^+$ to Br-C$^+$ neurons. Therefore, the Cas/Svp-dependent temporal control pathway seems to use different downstream targets to regulate the properties of the neuroblast and its progeny.

With their new study, Maurange et al. (2008) show that the transient expression of temporal regulators can have lasting effects on both the proliferation of the neuroblast and the cell fate of the progeny it produces. This work generates a number of intriguing questions. What are the common targets of Cas and Hb that regulate "young" stem cell identity and have the potential to induce seemingly indefinite proliferation? How does Svp counteract these factors to bring about the aging of neuroblasts? Do the persistent adult neuroblasts generated by stalling temporal progression still have the capacity to generate later-born Br-C$^+$ neurons? It will be interesting to see whether inducing a pulse of Svp expression in these persistent adult neuroblasts drives them through their normal temporal progression such that they switch from Chinmo$^+$ to Br-C$^+$ neuron production and eventually initiate a terminal division. In addition, *Drosophila* neuroblasts are known to lose volume with each division and shrink as they approach quiescence in the embryo (Hartenstein et al., 1987) or terminal division in the pupa (Maurange et al., 2008). Given this, how do the temporal control mechanisms explored by Maurange et al. (2008) regulate the size of neuroblasts, and what role might this regulation play in cell-cycle exit? The new work suggests that manipulating the temporal identity of neural stem cells might be a fruitful way to engineer the behavior of these cells in a controlled manner. It will be of great interest to see what roles analogous temporal factors play in the neural stem cells of the developing vertebrate CNS.

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Plant Evolution: TALES of Development

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TALE homeodomain proteins regulate development in many eukaryotes. Now, Lee et al. (2008) report that two TALE homeodomain proteins control zygote development of the unicellular green alga *Chlamydomonas*. This implicates TALE gene loss and diversification in the evolution of new diploid body plans that appeared when land plants evolved from algal ancestors over 450 million years ago.

The life cycle of sexually reproducing organisms comprises both haploid and diploid stages. In the green alga *Chlamydomonas reinhardtii*, both haploid and diploid phases of its life cycle are unicellular—the fusion of haploid cells (gametes) leads to the formation of a diploid cell (zygote) that then undergoes meiosis to regenerate more haploid individuals. The life cycles of land plants differ from that of *Chlamydomonas* in that they comprise multicellular haploid (gametophyte) and multicellular diploid (sporophyte) stages. In seed plants, for example, the diploid phase of the life cycle is dominant and displays greater morphological diversity than the haploid stage. Land plants are derived from a group of algae in which the diploid phase consists of only a zygote, as is the case in *C. reinhardtii*. Little is known about the specific factors that control the development of the earliest stages of the green plant life cycle. Elucidating the genetic

basis of zygote development in *C. reinhardtii* may shed light on the genetic changes underpinning the evolution of the diploid green plant body plan. In their new study in this issue, Lee et al. (2008) provide insight into the diploid program of development in *Chlamydomonas* with implications for understanding the evolution of land plants from green algae.

C. reinhardtii has two mating types: *plus* and *minus*. The homeodomain proteins Gsp1 and Gsm1 are expressed in the *plus* and *minus* gametes, respectively, and are localized in the cytoplasm (Zhao et al., 2001; Lee et al., 2008). Lee et al. now show that at fertilization when the *plus* cell fuses with the *minus* cell, Gsm1 and Gsp1 form dimers and move into the diploid nucleus where they direct development of the *Chlamydomonas* zygote. Both the constitutive expression of *GSM1* in *plus* vegetative cells (that also express *GSP1*) and the overexpression of *GSP1* in *minus* vegetative cells (that also express *GSM1*) could initiate zygote development. Furthermore, constitutive expression of *GSM1* and *GSP1* in diploid vegetative cells results in meiosis and spore formation. Thus, coexpression of *GSM1* and *GSP1* is sufficient to program development of the *Chlamydomonas* zygote.

Given that Gsm1 and Gsp1 appear to be master regulators of the diploid phase of development in the *Chlamydomonas* life cycle, what is their relationship to similar proteins in land plants where the zygote forms a multicellular diploid sporophyte? Gsm1 and Gsp1 are members of the TALE (three amino acid length) superclass of homeodomain proteins found in land plants that are known to be important in development. TALE proteins such as the KNOX class I proteins, KNOTTED and SHOOTMERISTEM LESS, are required for the development of the shoot apical meristem in the diploid phase of the seed plant life cycle; meanwhile, the protein BELLRINGER also controls aspects of diploid shoot development (Byrne et al., 2003; Hake et al., 2004; Barton and Poethig, 1993).

Lee et al. undertook a phylogenetic analysis comparing the protein sequences of Gsm1 and Gsp1 with TALE homeoproteins, including the KNOX and BELL proteins, from different land plants. They found that Gsm1 is a member of the KNOX class II homeodomain proteins that have been conserved between algal and plant lineages. They also found that *GSP1* is related to the BELL homeodomain proteins, although surprisingly, *Gsp1*-like BELL proteins seem to have disappeared from the genomes of the land plants they examined. Could this marked gene loss in land plants have evolutionary implications? How might the evolution of TALE genes from algal to plant lineages have resulted in the striking morphological diversity of land plants? Lee et al. (2008) hypothesize that initially, land plants inherited their TALE genes from algal ancestors where they regulated the development of the zygote. However, during or just prior to the emergence of the land plants, the *GSP1* gene was lost and this allowed the land plants to escape from the constraint of the algal life cycle "rut." This loss was accompanied by an increase in the diversity of the KNOX and the BELL classes of TALE homeodomain proteins that control development of multicellular diploid land plants. Given the ability of these two protein classes to form heterodimers, an increase in the number of homeodomain proteins would have meant that there was an increased potential for forging new protein interactions, with each protein combination controlling a discrete developmental pathway. So, Lee et al. propose that the loss of one gene and the concomitant diversification of other TALE members may account, in part, for the diversity of body plans observed in diploid land plants. This implies that the diversity of haploid land plant body plans may be controlled by something other than the TALE proteins. These regulators remain to be identified.

Other mechanisms may have also contributed to the evolution of morphological variation in the dominant diploid sporophyte, which occurred 350 and 410 million years ago (Kenrick and Crane, 1997). Some of the genes that control diploid development in seed plants may have been recruited from the haploid gametophyte (Menand et al., 2007). According to this model, some genes such as *ROOT HAIR DEFECTIVE6* (which controls the formation of tip-growing cells with rooting function) would have been active in the gametophyte of the earliest land plants. Then, as the diploid phase of the plant life cycle became morphologically more complex, these genes became active in the sporophyte, contributing to the increased diversity of the sporophyte. This finding together with the Lee et al. (2008) study suggests that the genes controlling diploid body plans of land plants had two origins: some evolved from ancestral genes that regulated zygote development in ancestral plants, and others may have had haploid-specific functions and were then recruited to control cellular diversity in the sporophyte.

Given that TALE homeodomain proteins regulate shoot and leaf development in the diploid phase of the life cycle in maize and the model plant *Arabidopsis thaliana*, it has been a mystery why these proteins do not control development of the leafy shoots of mosses (Kenrick and Crane, 1997; Singer and Ashton, 2007). Mosses are closely related to the earliest diverging lineages of land plants (Singer and Ashton, 2007). The leafy shoots of mosses (superficially similar to those of vascular plants) develop in the haploid phase of the moss life cycle, but the TALE proteins control the development of the diploid phase of the life cycle that has no meristem and lacks leaves (Singer and Ashton, 2007; Sano et al., 2005). Together with the findings of Lee et al., these observations suggest that TALE homeodomain proteins control diploid-specific aspects of the green plant life cycle regardless of morphology.

From the important roles played by TALE homeodomain proteins in diploid zygote development in *C. reinhardtii*, we might predict that the TALE proteins are also required for development of the land plant zygote. If true, then plants lacking a full complement of genes encoding TALE homeodomain proteins should not develop beyond the zygote stage, that is, development would cease as soon as the zygote forms with no further development into the sporophyte. Although such defective zygotic phenotypes have not yet been described, they may well be worth looking for.

The findings of Lee et al. suggest a model for the evolution of the morphologically complex sporophyte of land plants from algal ancestors. This model involves the loss and diversification of

genes with ancestral zygotic functions and the recruitment of genes that had been active in the haploid phase of the life cycle of ancestral plants. Thus, evolution of the TALE family of homeodomain proteins may lie behind the transformation of single-celled algal zygotes into the largest multicellular organisms to ever exist on Earth. That is quite an impressive claim for a small group of transcription factors, even if they are homeodomain proteins.

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